

## EFFECTS OF SHADING ON NURSERY GROWN ACACIA SEEDLINGS

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### ABSTRACT

This paper describes the effects of shading on four species of phyllodinous Australian acacias (Mimosidae) naturalised in the South Western Cape: *A. cyclops* A. Cunn. ex G. Don., *A. longifolia* (Andr.) Willd., *A. melanoxylon* R. Br. and *A. saligna* (Labill.) Wendl. Seedlings compensated for a 75 % reduction in light intensity by retaining their juvenile leaves longer, and by producing larger, more horizontally orientated phyllodes or leaves. The stems of the shaded plants were etiolated, and their root areas and root and shoot dry masses were less than those of plants grown in full sunlight. *A. melanoxylon* was the most, and *A. cyclops* the least shade tolerant species. Shading, achieved by the use of "smother crops" or by heaps of brushwood, may prove effective in the control of acacia regeneration, provided that at least 90 % light reduction could be obtained.

### UITTREKSEL

#### DIE INVLOED VAN SKADUWEE OP GEKWEEKTE ACACIA SAAILINGE

Die invloed van skaduwee op vier Australiese akasias (Mimosidae) met fillodes en wat in die Suidwestelike Kaap genaturaliseer is word beskryf: *A. cyclops* A. Cunn. ex G. Don., *A. longifolia* (Andr.) Willd., *A. melanoxylon* R. Br. en *A. saligna* (Labill.) Wendl. Saailinge het vir 'n 75 % verlaging ligintensiteit gekompenseer deur hulle eerste blare langer te behou en deur groter, meer horisontaal georiënteerde fillodes of blare voort te bring. Die stamme van die plante in skadu was geëtioloerd en hul wortelareas en wortel en stingel droë massa was minder as die van plante wat in volle son gekweek is. *A. melanoxylon* het die meeste en *A. cyclops* die minste skadu-toleransie getoon. Beskaduwing deur "smoorgewasse" of deur hope kreupelhout mag effektief blyk te wees om die regenerasie van akasia te beheer mits daar ten minste 90 % lig vermindering te weeg gebring kan word.

### INTRODUCTION

Some of the Australian *Acacia* species introduced to South Africa during the mid-nineteenth century have become naturalised, and are now considered to be problem plants on disused land and in the indigenous vegetation of the South Western Cape (Taylor, 1975; Hall & Boucher, 1977). After the removal of unwanted acacia thickets by fire or felling, the regeneration is generally controlled by herbicide treatment, slashing or weeding. An eco-

mical control program less damaging to the remaining indigenous plants and to the environment is needed.

Methods suitable for controlling shrub encroachment in grasslands, such as the use of browsing animals, or annual burns cannot be considered for use in the shrubby Fynbos which grows in shallow soil on steeply sloping ground. In their natural habitats in Australia or in Africa, there is very little acacia seedling regeneration beneath the canopy of mature acacia trees (Howard, 1974; Obeid & Seif el Din, 1970). There is also little or no regeneration under thickets or plantations of acacias growing as exotics (Donald, unpubl.; Milton, unpubl.), and acacia seedlings rarely survive under closed canopies of grasses (Brown & Booysen, 1967) or trees and shrubs (Roux & Middlemiss, 1963; Gilbert, 1959; Howard, 1974; Noble & Slatyer, 1977).

Lack of acacia seedling regeneration under a canopy could be due to either enforced dormancy, or to low seedlings survival rates. The latter is the more likely alternative since acacia seeds can germinate in the dark (Preece, 1971), and numerous seedlings have been seen under the deep shade of acacia thickets during the rainy season, few of which survive.

A number of factors may be responsible for the death of the acacia seedlings growing beneath taller plants: competition for water and nutrients or light, susceptibility to pathogens or inhibition by chemicals released by the roots or litter of dominant plants. The fact that heaps of brushwood control acacia regeneration as effectively as cover provided by living trees (Milton, unpubl.) indicates that the failure of seedlings to survive under a canopy is directly related to shading. This is not unexpected in the genus *Acacia*, where most of the species are heliophilous members of the early stages of succession (Weisser & Marques, 1979; Brown & Booysen, 1967; Noble & Slatyer, 1977; Pedley, 1978).

If shade could be used to control regeneration, it would have the advantage of disturbing the soil and remnant vegetation less than would mechanical methods. Shading has been used to control such weeds as *Stipa trichotoma* Nees and *Baccharis halimifolia* L. (Wells, 1977; Panetta, 1977).

This study is concerned with the effects of shade alone on the growth and morphology of acacia seedlings. In the experimental work predation, competition and allelopathy were eliminated or equalised as far as was possible.

## METHODS

### *Nursery experiments*

Locally collected seed of the four *Acacia* species were pretreated with hot water, germinated in petri dishes, and then planted singly in nursery bags. Clay-loam was the potting medium for *A. longifolia* (Andr.) Willd. and *A. melanoxylon* R.Br., but *A. cyclops* A.Cunn. ex G.Don. and *A. salig-*

na Labill.) Wendl. were planted in Cape Flats sand. These are the substrates normally found in habitats infested by the respective *Acacia* species. Both media had been sieved to facilitate the extraction of the root systems for growth evaluation.

The nursery bags were arranged in two sets on plastic sheets. One set was placed under a frame covered with black nylon shade-cloth which excluded 75 % of the light and reached the ground on all sides. The other set was set out in the open away from the shade of trees or buildings.

### Measurement of parameters

Seedlings were harvested 3, 4, 6, 8, 10 and 15 months after germination.

Root systems were extracted by washing the decanted plant over 1 mm plastic mesh. Root length was estimated using a method adapted from Rowse & Phillips (1974). Washed roots were spread out on a plastic sheet on which had been printed a grid of black lines one or two centimetres apart. The root/grid-line intersections were counted, and an estimate of root length was obtained from equation (1):-

$$L = \frac{1}{2} \pi D/2. N \dots\dots\dots (1)$$

where L is the estimated root length; D is the size of the grid squares and N is the number of root/grid-line intersections. This method gave results which compared favourably with results obtained by measuring each rootlet with dividers and ruler.

The average size of a photosynthetic organ (based on measurements of five mature leaves per plant) was calculated from the product of length, breadth, and a factor 'C' estimated to compensate for its non-rectangular shape. 'C' = 0,5 for the fusiform phyllodes of *A. saligna*, 0,6 for pinnate leaves, and 0,7 for the phyllodes of *A. cyclops*, *A. longifolia* and *A. melanoxylon*.

The total photosynthetic area was calculated by multiplying the mean leaf or phyllode area by the number of these organs on the plant. This statistic probably represents only half the actual photosynthetic area, because the dorsal and ventral surfaces of phyllodes appear to be similar.

In assessing the orientation of a leaf or phyllode, inclination but not rotation, was measured (Figure 1). The angle between the axis of the leaf or phyllode, and the vertical, gave an indication of verticality, 0° being vertical and 90° horizontal. This measurement was independent of stem angle, an important consideration in the case of lateral branches and tilted leader shoots.

After all other parameters had been measured, root and shoot were separated, oven-dried at 100 ° C for 24 hrs, and then weighed.

Fig. 1

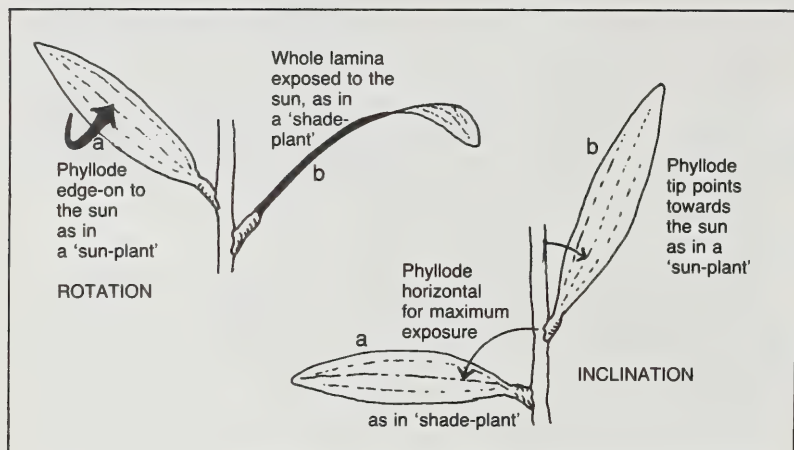


FIG. 1.

Foliage orientation, showing: ROTATION with phyllode (a) edge-on to the sun and (b) with lamina facing the sun, and INCLINATION with phyllode (a) near horizontal and (b) near vertical.

#### Relative growth rate . . . (R.G.R.)

R.G.R. was calculated using an equation (2) from Evans (1972):

$$\text{R.G.R.} = \frac{\log e_1 W - \log e_2 W}{_2T - _1T} \dots\dots\dots (2)$$

where  $_2W$  and  $_1W$  are the dry weights at the beginning and end of the harvesting period  $_1T$  to  $_2T$ , and the units are grams  $\text{g}^{-1}$  month $^{-1}$ .

#### Field studies

The relative light intensity under the shade of an isolated tree and under heaps of brushwood was measured using a photographic light meter (Sekonic Studio). Paired measurements were made a few seconds apart in shade and in the open. Light intensity in shade is expressed as a percentage of that in the open.

The heights of labelled *A. melanoxylon* seedlings growing under a parent tree, and of others in an open site, were measured at monthly intervals over a



period of 18 months. The results are of interest, as the possible occurrence of allelopathy, competition, predation and drought stress could not be controlled in the field.

## RESULTS

### *Growth rates of the four acacia species*

Relative growth rates of self-established seedlings measured in the field during their second year (Table 1) suggest that *A. saligna* grows faster than the other three species. However, both *A. saligna* and *A. longifolia* may be over 2 m tall within 2 years of germination.

The rapid height growth of these acacia seedlings means that they overtop Fynbos species 12–24 months after a fire, and eventually suppress this light-demanding indigenous vegetation (Figure 2). In deep shade (10 % of sunlight) *A. melanoxylon* seedlings remained stunted (Figure 3) and their R.G.R. was only 14 % that of seedlings growing in the open (Table 1).

### *The effects of shading on acacia seedling growth-habit and morphology*

Figures 4 and 5 illustrate the difference between acacia seedlings grown in full sunlight and those grown in one quarter sunlight. Shade-plants (Figure 4) are taller, and have retained their apical dominance for longer than plants grown in the open. The latter often develop prostrate or slanted leader shoots, and have many lateral shoots near the stem base. The stems of the sun-plants are red or yellow when young, rapidly becoming brown and woody with age; those of shade-plants remain green and pliable.

In the open, *A. melanoxylon* develops its first phyllodes at eight months, whereas in the shade it bears only pinnate leaves until it is about one year old. *A. cyclops*, *A. longifolia* and *A. saligna* seedlings develop their first phyllodes at about four months, whether grown in the sun or in the shade, but juvenile pinnate foliage, which has normally been lost by six months, is retained for up to 10 months in the shade.

The foliage of shade-plants is a light grassy green, their laminae thin-textured, broad, and in the case of *A. saligna*, undulating; those of sun-plants are relatively narrow, leathery and dark green, glaucous or red-tinted. The phyllodes and leaves of all species are held almost vertical in sun-plants, but in shade tend to droop or to be held horizontally (Figure 4). Notice that the phyllodes of the sun-plants are seen broad-side-on, while many shade-plant phyllodes are presented edge-on to the camera. Phyllodes can apparently be rotated so as to present only their margins to the sun (sun-plants) or the entire upper surface of the lamina (shade-plants).

Poor root development was a feature of shaded plants of all species and was obvious from the first harvest until the last root harvest at 10 months.

TABLE 1.  
Growth of acacia seedlings in the field during their second year

| Species<br>Site                       | <i>A. cyclops</i> <sup>1</sup><br>coastal | <i>A. longifolia</i><br>inland | <i>A. melanoxylon</i><br>inland | <i>A. melanoxylon</i><br>inland <sup>2</sup> | <i>A. saligna</i><br>coastal | <i>A. saligna</i><br>inland |
|---------------------------------------|-------------------------------------------|--------------------------------|---------------------------------|----------------------------------------------|------------------------------|-----------------------------|
| R.G.R.<br>month) . . . . .            | 0,284                                     | 0,342                          | 0,306                           | 0,043                                        | 0,449                        | 0,443                       |
| Height<br>(cm/mth) . . . . .          | 3,6                                       | 13,6                           | 7,7                             | 1,7                                          | 13,1                         | 14,8                        |
| Tot. height at 2<br>yr (cm) . . . . . | —                                         | 213                            | 142                             | 29                                           | 207                          | 225                         |

<sup>1</sup> age unknown

<sup>2</sup> deep shade (10 % normal sunlight)

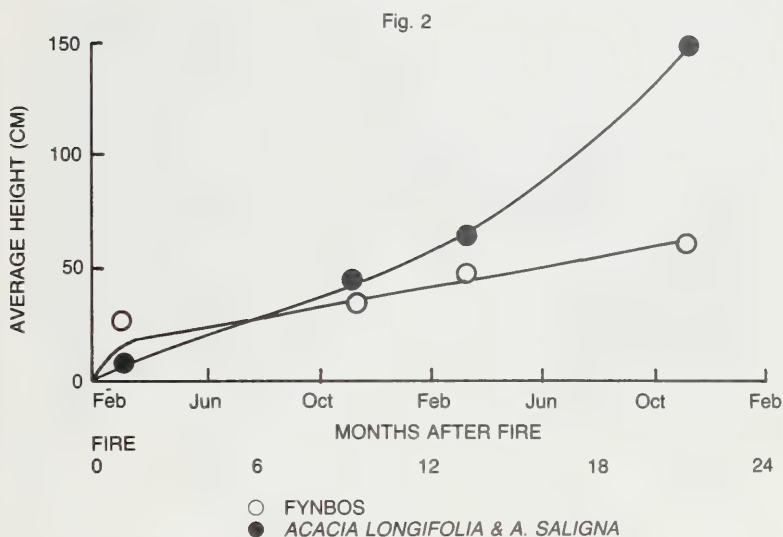


FIG. 2.

Cumulative height growth of *Acacia saligna* and *A. longifolia* seedlings, and Fynbos shrubs after fire. (Data from a single 100 m<sup>2</sup> plot on the burned lower north-facing slopes of the Constantiaberg, Cape Peninsula).

The effects of shading on the root systems of three and four month old seedlings are illustrated in Figure 5; notice too the advanced development of nodules on the sun-plants.

#### *Quantitative assessment of shading effects on acacia seedlings*

Analysis of variance tests were used to compare sun- and shade-plants for all parameters measured at each harvest. The results are summarised in Appendix 1.

**Foliage characters.** Of the foliage parameters tested, pinnate leaf number and foliage orientation were the most light sensitive (i.e. these parameters usually differed significantly between sun- and shade-plants). Shade-plants tended to retain their juvenile pinnate leaves longer. Leaves and pinnules of shade-plants were set further from the vertical (44°) than were those of sun-plants (23°). Differences in the areas and sizes of photosynthetic organs were seldom significant, but there was a tendency for those of shade-plants to be fewer but larger. The total photosynthetic area of *A. melanocylon*

Fig. 3

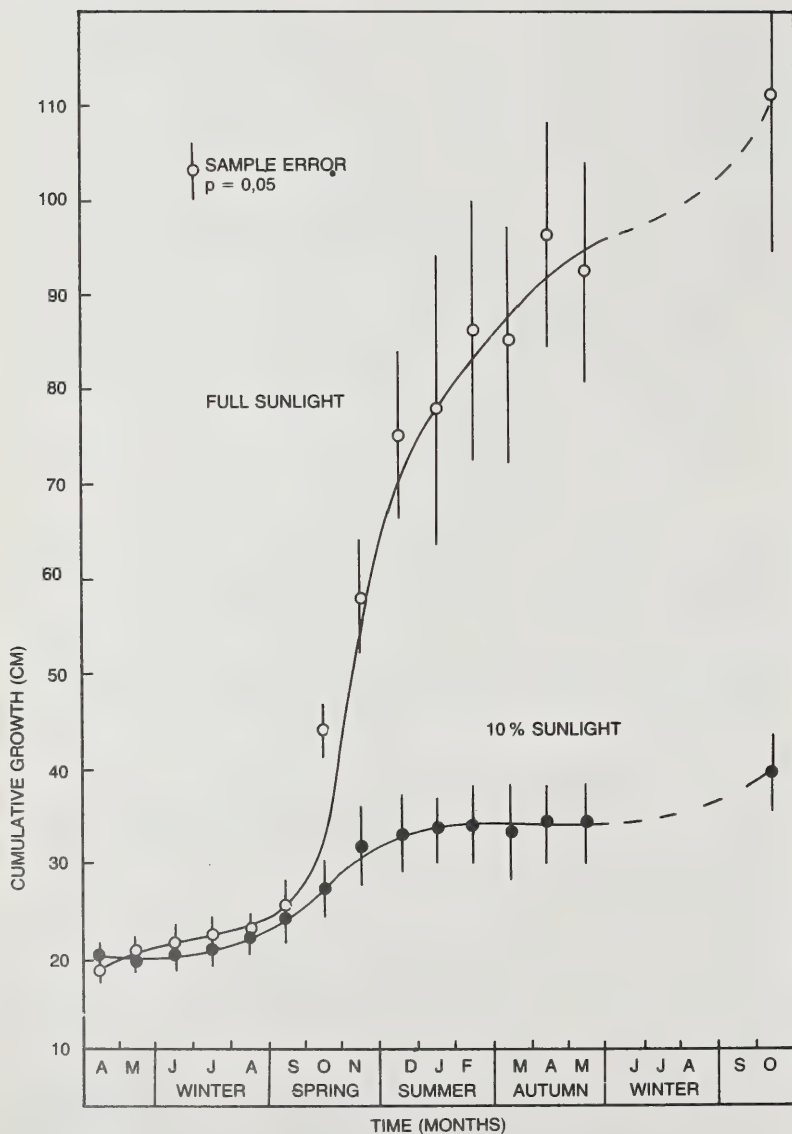


FIG. 3.

Height growth of self-established *A. melanoxylon* seedlings in the field, showing the effect of deep shade on the growth rate of seedlings.

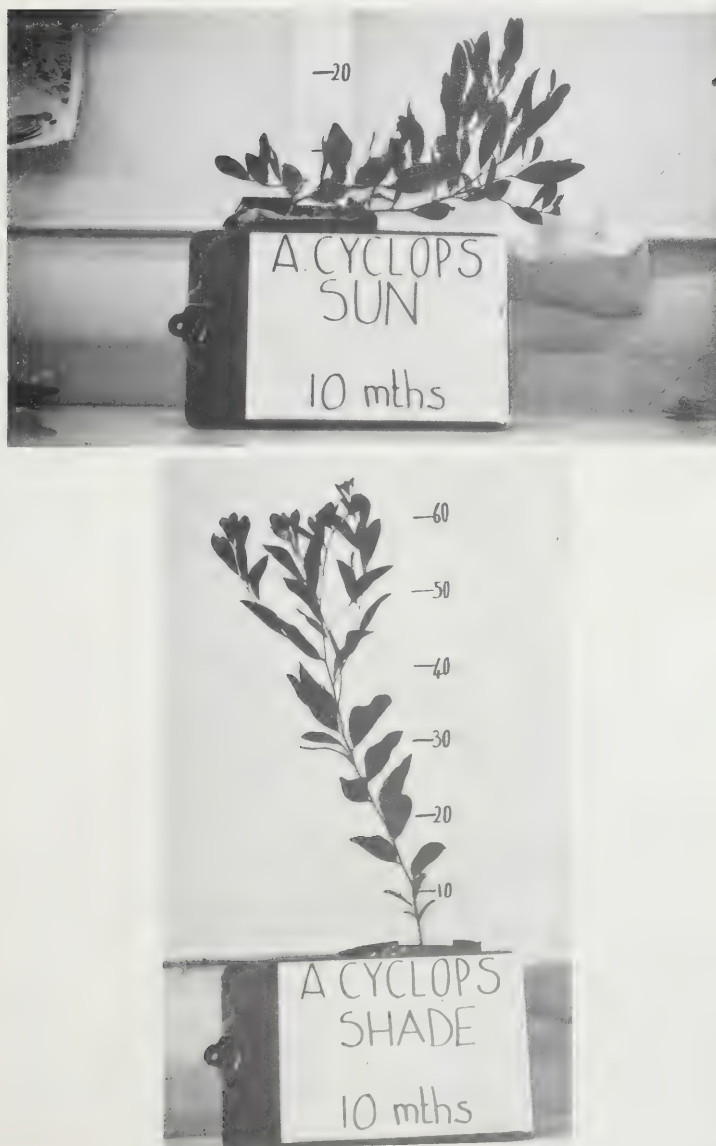


FIG. 4.

Sun- and shade-plants of four *Acacia* species photographed at four months. Note that sun-plants are shorter and more branched. They have more phyllodes, and these are held stiffly, edge-on to the sun in a near vertical position.



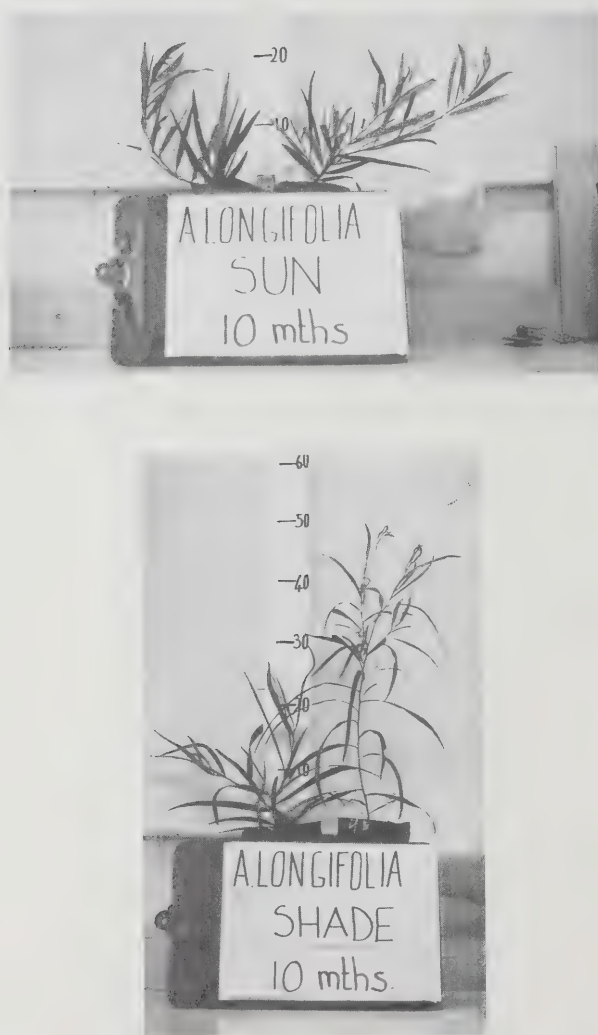


FIG. 4. (Continued)

Sun- and shade-plants of four *Acacia* species photographed at four months. Note that sun-plants are shorter and more branched. They have more phyllodes, and these are held stiffly, edge-on to the sun in a near vertical position.

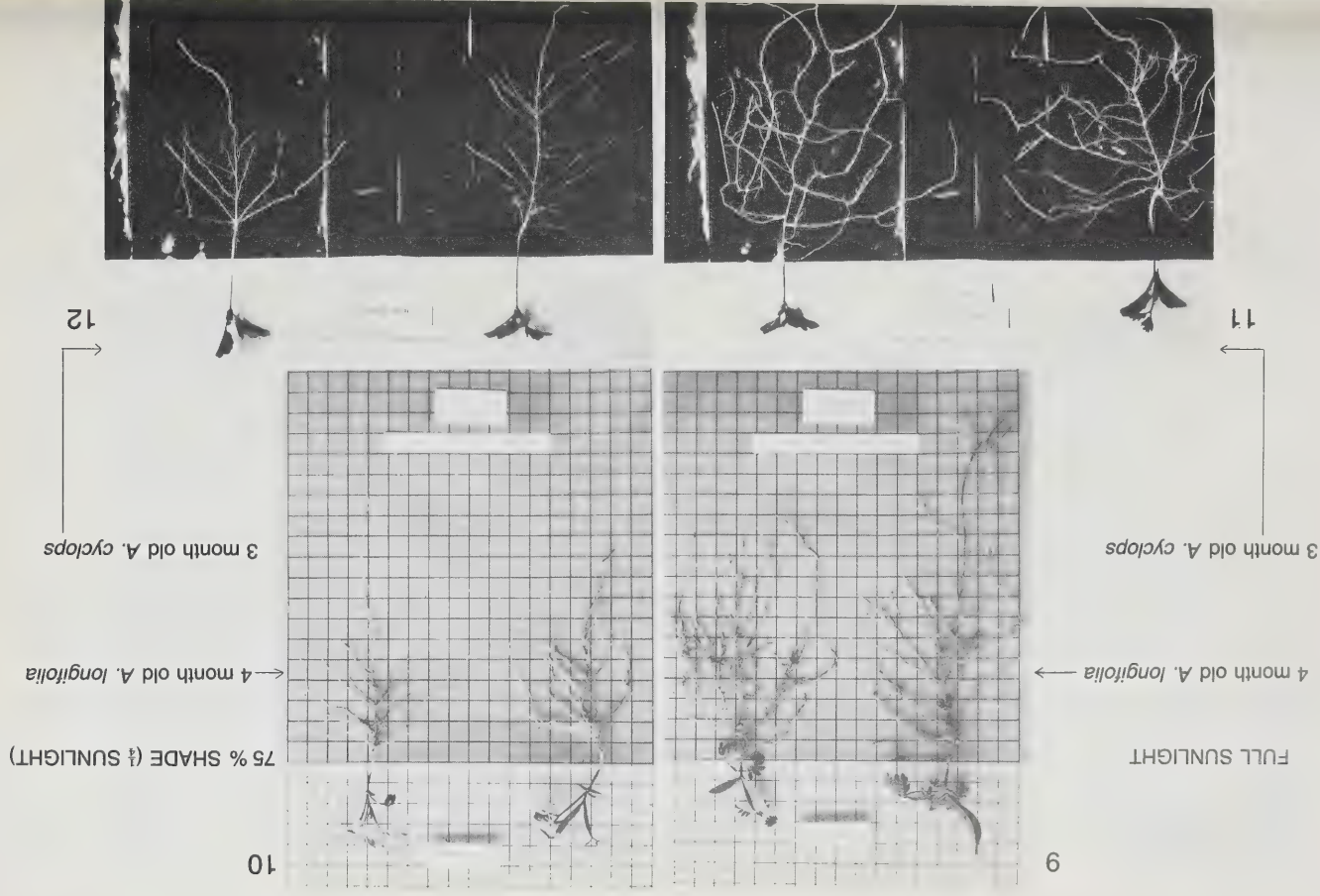


FIG. 4. (Continued)

Sun- and shade-plants of four *Acacia* species photographed at four months. Note that sun-plants are shorter and more branched. They have more phyllodes, and these are held stiffly, edge-on to the sun in a near vertical position.

Fig. 5

The effects of shading on the early development of the root system of *Acacia* seedlings.  
Note the relative scarcity of lateral roots and nodules on shaded plants.



shade-plants was greater, but that of *A. cyclops* less than that of their counterparts growing in the open, suggesting that the latter species was unable to compensate for light reduction by foliage expansion.

**Stem characters.** Shading resulted in etiolation of all four species. This trend was consistent, though, due to undersampling, not highly significant (Appendix 1). Above ground production (shoot dry mass) of *A. melanoxylon* shade-plants did not differ significantly from that of sun-plants, but in other species, notably *A. cyclops*, shoot production was less in the shade. Consistent, if not significant, reduction was recorded in the stem basal circumference and the number of lateral shoots of shade-plants of all species.

**Root characters.** Root production (in terms of dry mass or surface area) was severely curtailed by shading in all species, and appeared to be the most light-sensitive parameter measured. Shade-plants also tended to produce fewer or small nodules, but nodule parameters were highly variable.

**Total dry mass production.** The dry mass of shade-plants was less than that of sun-plants. This trend was highly significant in *A. cyclops* and *A. longifolia*, but not significant in *A. melanoxylon*.

**Shoot/root dry-mass ratio.** This is consistently larger in shade-plants implying that shoot development proceeds at the expense of root development when light is limited. Treatment differences in the shoot/root ratio (Table 2) were more marked in *A. saligna* and *A. melanoxylon*, which maintained good shoot growth in the shade, than in *A. cyclops* and *A. longifolia*, where

TABLE 2.  
Mean shoot/root dry-mass ratios for each harvest.<sup>1</sup>

| Age at harvest<br>(months)     | <i>A. cyclops</i> |       | <i>A. longifolia</i> |       | <i>A. melanoxylon</i> |       | <i>A. saligna</i> |       |
|--------------------------------|-------------------|-------|----------------------|-------|-----------------------|-------|-------------------|-------|
|                                | Sun               | Shade | Sun                  | Shade | Sun                   | Shade | Sun               | Shade |
| 3                              | 1,72              | 2,37  | 0,87                 | 1,06  | 0,87                  | 1,57  | 1,12              | 1,03  |
| 4                              | 2,00              | 2,61  | 0,79                 | 1,16  | 1,03                  | 1,11  | 1,13              | 2,78  |
| 6                              | 2,19              | 2,69  | 1,26                 | 2,50  | 0,97                  | 1,49  | 1,44              | 2,63  |
| 8                              | 2,35              | 4,93  | 1,86                 | 3,21  | 1,80                  | 2,62  | 1,65              | 2,18  |
| 10                             | 2,29              | 3,78  | 1,82                 | 2,93  | 1,04                  | 2,49  | 1,27              | 2,67  |
| Significance<br>between months | *                 | ns    | **                   | **    | **                    | **    | ns                | ns    |

<sup>1</sup> Significant differences between treatments are underlined ( $P = 0,05$ ).

Significant differences between months are indicated as follows:

ns = not significant

\* = significant at 0,05 level

\*\* = significant at 0,01 level

shading reduced both shoot and root production. For all four species and under both treatments the shoot/root dry-mass ratio increases as the seedlings grow. Other authors have also found that root growth takes precedence over shoot growth during the early early stages of seedling growth (Panetta, 1977; Withers, 1979), and have suggested that, by stunting the root system, shading causes moisture stress, which leads to the death of seedlings.

*The relationship between total photosynthetic area and total dry mass.*

Shading affects both the photosynthetic area and the total dry mass of acacia seedlings. The increase or decrease in the total photosynthetic area (TPA) or in the total dry mass (TDM) of a shade-plant relative to a sun-plant was calculated as follows:-

$$\Delta X = \frac{{}_2X - {}_1X}{{}_1X} \dots\dots\dots (3)$$

where  $\Delta X$  = difference in TPA or TDM between shade-and sun-plants relative to sun-plant

${}_1X$  = TPA or TDM of a sun-plant

${}_2X$  = TPA or TDM of a shade-plant

The regression of mean  $\Delta$  TDM values on mean  $\Delta$  TPA values, obtained by equation 3, arranged the species linearly in order of their relative 'efficiency' in shade. The linear relationship was not unexpected as photosynthetic area and dry mass are linearly related (Evans, 1972).

In order to illustrate area/mass relationships within as well as between species, all data for each species are plotted, as well as the mathematically fitted curves based on the mean for each species (Figure 6).

*A. melanoxylon*, a sub-climax species, in which shade-plants were found to have a larger total photosynthetic area than sun-plants, suffer minimal fall-off in dry matter production when growing in the shade. The converse is true for *A. cyclops*, a coastal pioneer. TPA was very variable in *A. saligna* and *A. longifolia*, but within these species there was a tendency for larger relative TPA reductions to be correlated with large relative TDM reductions.

Although *A. melanoxylon* was not the most productive species in absolute terms when grown in the shade, its ability to maintain in reduced light at a level similar to that in full light, indicates that it is the most shade tolerant of the four species examined in this study.

Fig. 6

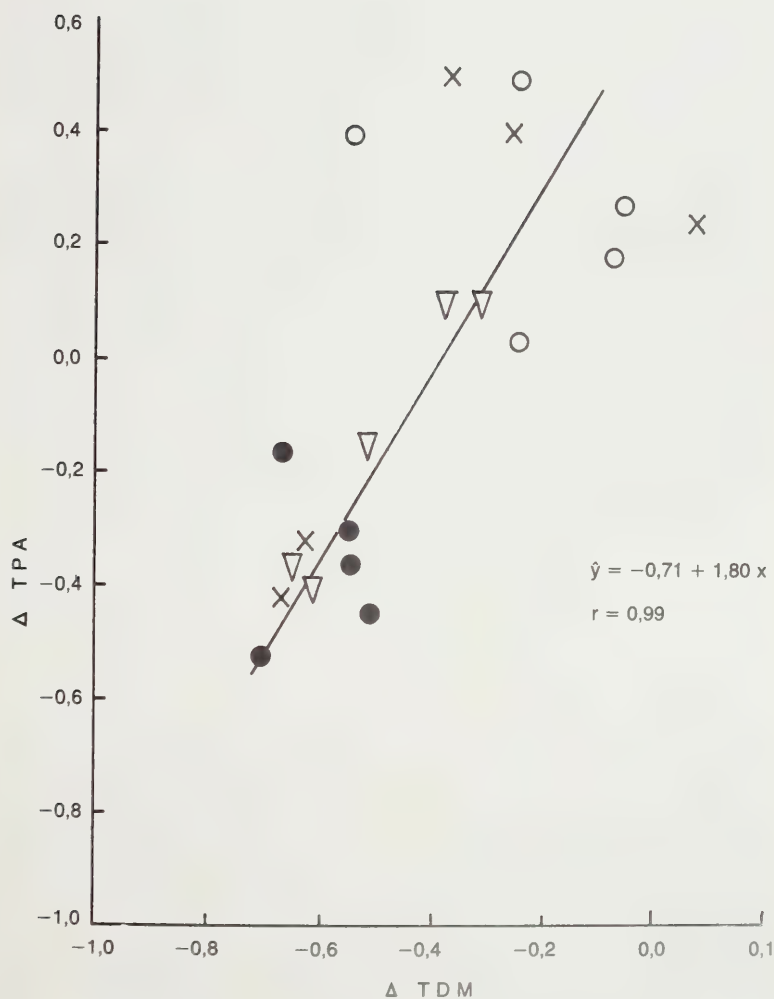


FIG. 6.  
Relative shade 'efficiency' of four species of *Acacia* as illustrated by the relationship between  $\Delta TDM$  and  $\Delta TPA$  values (equation 3). Data are given in full in Appendix 2. Curve is fitted to the mean values for each species.



## DISCUSSION

If one accepts the theory of natural selection, one would expect that the shade tolerance limits of a species would enable it to function most efficiently in its normal habitat. When forced to grow outside its normal range of light intensity a plant can compensate by increasing or decreasing attributes such as the size of its leaves, the amount of chlorophyll that they contain, or the angle at which they intercept the light.

*Acacia* seedlings react to shading in much the same way as seedlings of other kinds of plants (Table 3). In moderate shade, they tended to produce fewer, larger, thinner textured leaves, orientated so as to intercept the maximum amount of light, and plants were generally etiolated and unbranched. The R.G.R. and dry matter production of shaded seedlings was relatively low, and their root systems were reduced and poorly nodulated.

The effects of extreme light reduction are not listed in Table 3. When light is reduced beyond the limits for a particular species, rates of respiration and photosynthesis are reduced so that the compensating morphology can no longer be maintained. Smaller leaves are produced, the growth rate decreases, and the plant remains dwarfed or dies without reproducing itself (Cameron, 1970; Ashton & Frankenberg, 1976; Withers, 1979; Evans, 1972; Panetta, 1977). The degree of shading at which leaves and total leaf areas are smaller rather than larger than those produced by the species in daylight, may indicate the shade tolerance of the species. Reduction in leaf area occurs below 42 % daylight in *Eucalyptus* spp. seedlings (Cameron, 1970; Withers, 1979), below 8 % in the seedlings of *A. pycnantha*, an understorey shrub in *Eucalyptus* woodland (Withers, 1979), and below 2 % for the seedlings of *Acmena smithii* growing beneath the parent canopy in tall closed forest (Ashton & Frankenberg, 1976).

*Acacia cyclops*, a shrub from the dunes of S.W. Australia (Seddon, 1972) was the least shade tolerant of the four species examined in this study. In 25 % daylight it had smaller phyllodes and significantly less total photosynthetic area than it had in the open. It also failed to retain its juvenile leaves in the shade, and its phyllodes were never held at an angle greater than 30° from the vertical. The inability of *A. cyclops* to compensate for reduced light accounts for the extreme differences in root and shoot dry mass between sun- and shade-grown seedlings.

*A. melanoxylon* which was found to be the most shade tolerant of the four *Acacia* species (Figure 6), produced only pinnate leaves in the shade, and these were held at an average angle of 50° from the vertical. This member of the pre-climax sere of the coastal forests of eastern Australia (Farrell & Ashton, 1978) suffers very little loss in dry matter production when grown in 25 % daylight. It requires a minimum of only 20 % daylight for normal

TABLE 3.

Summary of shade-plant characteristics relative to those of sun-plants. The symbols +; =; -; indicate increase, equality or decrease of a parameter in a shade-plant relative to that of a sun-plant. Symbols in parenthesis are based on observations only. Blanks indicate a lack of information.

| Species              | <i>Acacia<br/>cyclops</i> | <i>Acacia<br/>longif.</i> | <i>Acacia<br/>melanox.</i> | <i>Acacia<br/>saligna</i> | <i>Acacia<br/>pycnantha</i> | Deciduous<br>hardwoods | <i>Eucalypt<br/>ssp.</i> | <i>Impatiens<br/>parviflora</i> | <i>Baccharis<br/>halimifolia</i> | General            |
|----------------------|---------------------------|---------------------------|----------------------------|---------------------------|-----------------------------|------------------------|--------------------------|---------------------------------|----------------------------------|--------------------|
| Seral stage          | early                     | mid                       | late                       | early                     | mid                         | late                   | late                     | late                            | early                            | -                  |
| Height               | +                         | +                         | +                          | +                         | +                           | +                      | +                        | +                               | +                                | +                  |
| Leaf/phyllode size   | +                         | =                         | +                          | =                         | +                           | +                      | +                        | +                               | +                                | +                  |
| Juvenile leaf no.    | +                         | +                         | +                          | +                         | +                           | +                      | +                        | +                               | +                                | +                  |
| Leaf thickness       | (-)                       | (-)                       | (-)                        | (-)                       | (-)                         | (-)                    | (-)                      | (-)                             | (-)                              | (-)                |
| Leaf/phyll no.       | (-)                       | (-)                       | (-)                        | (-)                       | (-)                         | (-)                    | (-)                      | (-)                             | (-)                              | (-)                |
| Verticality          | -                         | =                         | -                          | =                         | -                           | -                      | =/-                      | -                               | -                                | -                  |
| Total foliage area   | -                         | =                         | +                          | =                         | +                           | -                      | -/+                      | -                               | -                                | +                  |
| Total chlorophyll    | pale                      | pale                      | pale                       | pale                      | -                           | -                      | -                        | -                               | -                                | -                  |
| Lateral shoot no.    | (-)                       | -                         | -                          | (-)                       | -                           | -                      | -                        | -                               | -                                | -                  |
| Stem base girth      | +                         | +                         | +                          | +                         | +                           | -                      | +                        | -                               | -                                | -                  |
| Internode length     | -                         | -                         | -                          | (-)                       | -                           | -                      | -                        | -                               | -                                | -                  |
| Photosynthetic rate  | -                         | =                         | =                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Relative growth rate | -                         | =                         | =                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Shoot dry mass       | -                         | -                         | -                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Root dry mass        | -                         | -                         | -                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Shoot/root ratio     | +                         | +                         | +                          | +                         | +                           | -                      | -                        | +                               | +                                | +                  |
| Nodule dry mass      | -                         | -                         | -                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Nodule number        | -                         | -                         | -                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Moisture content     | +                         | +                         | +                          | +                         | +                           | -                      | -                        | -                               | -                                | -                  |
| Root surface area    | -                         | -                         | -                          | -                         | -                           | -                      | -                        | -                               | -                                | -                  |
| Source of data       |                           |                           | this study                 |                           | Withers<br>1979             | Logan<br>1965          | Cameron<br>1970          | Evans<br>1972                   | Panetta<br>1977                  | Daubenmire<br>1947 |

growth (Donald, unpubl.) and can survive in 8 % daylight (Phillips, 1928), although severely stunted in deep shade (Figure 2).

The significance of shade tolerance for management is that, while *A. melanoxylon* seedlings are suppressed in tall climax rain-forest (Howard, 1974; Ashton & Frankenberg, 1976) in Australia and likewise in the indigenous forest of the S. and S.W. Cape (Phillips, 1928; Donald, unpubl.), they can become established in marginal and disturbed forest. Both *A. longifolia* and *A. saligna* showed considerable variation in their reaction to shading (Figure 6). It is possible that these species have a generalist strategy which has enabled them to become naturalised in a wider variety of habitats than *A. cyclops* and *A. melanoxylon*.

#### CONCLUSION AND MANAGEMENT IMPLICATIONS

The seedlings of all the *Acacia* species tested survived for 15 months in 25 % daylight, and by this time had reached a height of 600 mm. A reduction of more than 75 % of incident light would be necessary for the suppression of any of these species.

Field observations suggest that 90 % to 95 % light reduction is adequate for the control of *A. cyclops* and *A. saligna* and probably also *A. longifolia*, since the seedlings of this species also fail to become established in thickets. Deeper shading may be necessary for the control of *A. melanoxylon*.

Shading can be achieved after felling the acacia trees by stacking the brushwood into heaps one or two meters high. Although the open areas between these stacks must be kept weeded of acacia seedlings, this control measure has the advantage of encouraging large populations of rodents which feed on the acacia seed under the brush and in the open. Brush heaps also offer perches for birds: potential vectors of indigenous seed. This method has been used with success on the dunes of the Goukamma Coastal Nature Reserve, S. Cape (Milton, unpubl.) and is recommended for sites subject to erosion where brushwood should be stacked in rows at right angles to the gradient.

To avoid mass germination of acacia seed lying dormant in the soil it is essential to exclude fire for many years, perhaps for over a century, once indigenous vegetation has been re-established. In mountain catchment areas this may conflict with Forestry Department policy, which prescribes burning of the vegetation on a 10 to 15 year rotation (Kruger, 1977).

It may also be possible to provide adequate shade by establishing 'smother crops'. Ideally these should be fast-growing, easily and cheaply established from seed, and unlikely to pose an additional threat to indigenous vegetation. Pioneer grasses such as *Avena fatua* L. and *Ehrharta villosa* Schult. f. grow vigorously on sites recently cleared of acacias. Early seral

Appendix 1  
Data summary for seedling shading experiments.

| Parameter                | Species                     | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | <sup>1</sup> Signif. |
|--------------------------|-----------------------------|------------|------------|-----|------|--------------|-----|------|----------------------|
|                          |                             |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |                      |
| Shoot<br>length<br>(cm)  | <i>A. cyclops</i>           | 3          | 3,5        | 5   | 35   | 4,3          | 5   | 5    | ns                   |
|                          |                             | 4          | 4,6        | 5   | 21   | 5,9          | 5   | 9    | *                    |
|                          |                             | 6          | 12,2       | 5   | 9    | 17,3         | 5   | 17   | ***                  |
|                          |                             | 8          | 23,5       | 2   | 9    | 43,5         | 2   | 10   | *                    |
|                          |                             | 10         | 36,5       | 2   | 10   | 67,0         | 2   | 46   | ns                   |
|                          | <i>A. longi-<br/>folia</i>  | 3          | 2,3        | 5   | 24   | 2,4          | 5   | 28   | ns                   |
|                          |                             | 4          | 2,0        | 5   | 26   | 2,8          | 5   | 10   | **                   |
|                          |                             | 6          | 5,6        | 5   | 38   | 6,9          | 2   | 49   | ns                   |
|                          |                             | 8          | 24,8       | 2   | 14   | 44,2         | 2   | 13   | ns                   |
|                          |                             | 10         | 31,0       | 2   | 5    | 36,0         | 2   | 64   | ns                   |
|                          |                             | 15         | 31,2       | 5   | 14   | 45,5         | 5   | 30   | ns                   |
|                          | <i>A. melan-<br/>oxylon</i> | 3          | 2,1        | 5   | 17   | 2,8          | 5   | 17   | *                    |
|                          |                             | 4          | 3,5        | 5   | 21   | 3,9          | 5   | 25   | ns                   |
|                          |                             | 6          | 8,1        | 5   | 34   | 16,1         | 5   | 53   | ns                   |
|                          |                             | 8          | 37,5       | 2   | 9    | 61,0         | 2   | 0    | **                   |
|                          |                             | 10         | 39,5       | 2   | 23   | 59,0         | 2   | 2    | ns                   |
|                          |                             | 15         | 36,5       | 5   | 10   | 54,5         | 5   | 27   | *                    |
|                          | <i>A. saligna</i>           | 3          | 1,2        | 5   | 14   | 1,5          | 5   | 10   | ***                  |
|                          |                             | 4          | 1,1        | 5   | 60   | 3,0          | 5   | 32   | ***                  |
|                          |                             | 6          | 2          | 5   | 46   | 10,9         | 5   | 55   | ns                   |
|                          |                             | 8          | 28,9       | 2   | 8    | 59,5         | 2   | 4    | ***                  |
|                          |                             | 10         | 36,0       | 2   | 43   | 65,0         | 2   | 0    | ns                   |
| Shoot<br>dry<br>mass (g) | <i>A. cyclops</i>           | 3          | 0,04       | 5   | 34   | 0,03         | 5   | 15   | **                   |
|                          |                             | 4          | 0,12       | 5   | 32   | 0,06         | 5   | 17   | ***                  |
|                          |                             | 6          | 1,05       | 5   | 22   | 0,34         | 5   | 26   | ****                 |
|                          |                             | 8          | 5,38       | 2   | 20   | 2,12         | 2   | 4    | ns                   |
|                          |                             | 10         | 11,40      | 2   | 37   | 5,95         | 2   | 77   | ns                   |
|                          |                             | 15         | 15,74      | 5   | 18   | 8,44         | 5   | 35   | ****                 |
| Shoot<br>dry<br>mass (g) | <i>A. longi-<br/>folia</i>  | 3          | 0,03       | 5   | 32   | 0,01         | 5   | 46   | **                   |
|                          |                             | 4          | 0,04       | 5   | 34   | 0,03         | 5   | 31   | ns                   |
|                          |                             | 6          | 0,45       | 5   | 40   | 0,20         | 5   | 70   | ns                   |
|                          |                             | 8          | 3,07       | 2   | 4    | 2,43         | 2   | 6    | *                    |
|                          |                             | 10         | 4,25       | 2   | 15   | 3,20         | 2   | 4    | ns                   |
|                          |                             | 15         | 8,10       | 5   | 22   | 7,00         | 5   | 63   | ns                   |
|                          | <i>A. melan-<br/>oxylon</i> | 3          | 0,02       | 5   | 10   | 0,02         | 5   | 32   | ns                   |
|                          |                             | 4          | 0,05       | 5   | 31   | 0,04         | 5   | 30   | ns                   |
|                          |                             | 6          | 0,26       | 5   | 39   | 0,29         | 5   | 36   | ns                   |
|                          |                             | 8          | 4,18       | 2   | 14   | 3,60         | 2   | 2    | ns                   |
|                          |                             | 10         | 4,65       | 2   | 17   | 2,85         | 2   | 37   | ns                   |
|                          |                             | 15         | 5,70       | 5   | 6    | 6,10         | 5   | 44   | ns                   |

<sup>1</sup> Level of significance \* = 0,5; \*\* = 0,25; \*\*\* = 0,1; \*\*\*\* = 0,05

| Parameter                                                           | Species                     | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signifi. |
|---------------------------------------------------------------------|-----------------------------|------------|------------|-----|------|--------------|-----|------|----------|
|                                                                     |                             |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |          |
| Mean <sup>2</sup><br>leaf or<br>phyllode<br>size (cm <sup>2</sup> ) | <i>A. saligna</i>           | 3          | 0,02       | 5   | 68   | 0,02         | 5   | 6    | ns       |
|                                                                     |                             | 4          | 0,11       | 5   | 47   | 0,05         | 5   | 32   | *        |
|                                                                     |                             | 6          | 1,17       | 5   | 52   | 0,49         | 5   | 59   | ns       |
|                                                                     |                             | 8          | 4,25       | 2   | 12   | 5,13         | 2   | 8    | ns       |
|                                                                     |                             | 10         | 10,70      | 2   | 74   | 8,75         | 2   | 35   | ns       |
|                                                                     |                             | 15         | 45,73      | 5   | 44   | 20,63        | 5   | 33   | ns       |
|                                                                     | <i>A. cyclops</i>           | 3          | 1,9        | 5   | 52   | 1,3          | 5   | 29   | ns       |
|                                                                     |                             | 4          | 2,1        | 5   | 21   | 2,0          | 5   | 36   | ns       |
|                                                                     |                             | 6          | 10,4       | 5   | 18   | 5,2          | 5   | 15   | ****     |
|                                                                     |                             | 8          | 8,7        | 2   | 11   | 10,3         | 2   | 28   | ns       |
|                                                                     |                             | 10         | 17,7       | 2   | 10   | 19,7         | 2   | 37   | ns       |
|                                                                     | <i>A. longi-<br/>folia</i>  | 3          | 0,9        | 5   | 43   | 0,8          | 5   | 84   | ns       |
|                                                                     |                             | 4          | 1,0        | 5   | 16   | 1,2          | 5   | 28   | ns       |
|                                                                     |                             | 6          | 2,8        | 5   | 36   | 3,3          | 2   | 42   | ns       |
|                                                                     |                             | 8          | 5,5        | 2   | 19   | 7,6          | 2   | 27   | ns       |
|                                                                     |                             | 10         | 9,6        | 2   | 26   | 12,9         | 2   | 1    | ns       |
|                                                                     |                             | 15         | 7,3        | 5   | 16   | 13,4         | 5   | 19   | ***      |
| Mean<br>leaf or<br>phyllode<br>size (cm <sup>2</sup> )              | <i>A. melan-<br/>oxylon</i> | 3          | 0,4        | 5   | 29   | 0,7          | 5   | 39   | ms       |
|                                                                     |                             | 4          | 1,1        | 5   | 36   | 1,6          | 5   | 36   | ns       |
|                                                                     |                             | 6          | 2,9        | 5   | 28   | 5,2          | 5   | 26   | ***      |
|                                                                     |                             | 8          | 3,7        | 2   | 40   | 10,1         | 2   | 28   | **       |
|                                                                     |                             | 10         | 7,1        | 2   | 12   | 16,1         | 2   | 11   | **       |
|                                                                     |                             | 15         | 6,7        | 5   | 16   | 17,9         | 5   | 30   | ****     |
|                                                                     | <i>A. saligna</i>           | 3          | 0,6        | 5   | 23   | 0,8          | 5   | 13   | *        |
|                                                                     |                             | 4          | 1,6        | 5   | 24   | 1,3          | 5   | 25   | ns       |
|                                                                     |                             | 6          | 13,5       | 5   | 30   | 5,1          | 5   | 42   | ***      |
|                                                                     |                             | 8          | 19,6       | 2   | 10   | 17,9         | 2   | 2    | ns       |
|                                                                     |                             | 10         | 21,5       | 2   | 27   | 38,4         | 2   | 13   | ns       |
|                                                                     | <i>A. cyclops</i>           | 3          | 2,8        | 5   | 30   | 2,2          | 5   | 21   | ns       |
|                                                                     |                             | 4          | 4,0        | 5   | 0    | 3,0          | 5   | 24   | **       |
|                                                                     |                             | 6          | 3,2        | 5   | 26   | 4,6          | 5   | 19   | *        |
|                                                                     |                             | 8          | 0,5        | 2   | 142  | 3,5          | 2   | 61   | ns       |
|                                                                     |                             | 10         | 0,5        | 2   | 142  | 2,0          | 2   | 0    | ns       |
| Pinnate<br>leaf<br>number                                           | <i>A. longi-<br/>folia</i>  | 3          | 3,8        | 5   | 12   | 2,6          | 5   | 21   | ***      |
|                                                                     |                             | 4          | 4,0        | 5   | 18   | 3,4          | 5   | 34   | ns       |
|                                                                     |                             | 6          | 4,4        | 5   | 26   | 4,9          | 2   | 0    | ns       |
|                                                                     |                             | 8          | 1,0        | 2   | 141  | 4,5          | 2   | 47   | ns       |
|                                                                     |                             | 10         | 0,0        | 2   | 0    | 4,0          | 2   | 0    | ****     |
|                                                                     |                             | 15         | 0,0        | 9   | 0    | 0,0          | 5   | 0    | ns       |

<sup>2</sup>length × breadth × shape factor

| Parameter                             | Species               | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signif. |
|---------------------------------------|-----------------------|------------|------------|-----|------|--------------|-----|------|---------|
|                                       |                       |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |         |
|                                       | <i>A. melanoxylon</i> | 3          | 4,2        | 5   | 20   | 3,8          | 5   | 22   | ****    |
|                                       |                       | 5          | 6,6        | 5   | 8    | 5,4          | 5   | 28   | ns      |
|                                       |                       | 6          | 19,8       | 5   | 19   | 12,0         | 5   | 16   | ****    |
|                                       |                       | 8          | 27,5       | 2   | 54   | 20,5         | 2   | 3    | ns      |
|                                       |                       | 10         | 35,5       | 2   | 2    | 32,5         | 2   | 37   | ns      |
|                                       |                       | 15         | 9,2        | 5   | 81   | 19,8         | 5   | 25   | *       |
| Pinnate<br>leaf<br>number             | <i>A. saligna</i>     | 3          | 5,0        | 5   | 14   | 5,2          | 5   | 87   | ns      |
|                                       |                       | 4          | 6,4        | 5   | 21   | 6,0          | 5   | 29   | ns      |
|                                       |                       | 6          | 1,4        | 5   | 109  | 5,0          | 5   | 32   | ***     |
|                                       |                       | 8          | 0,0        | 2   | 0    | 1,5          | 2   | 47   | ns      |
|                                       |                       | 10         | 0,0        | 2   | 0    | 0,0          | 2   | 0    | ns      |
| Phyllode<br>number                    | <i>A. cyclops</i>     | 3          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 4          | 0,4        | 5   | 138  | 0,0          | 5   | 0    | ns      |
|                                       |                       | 6          | 5,8        | 5   | 22   | 4,0          | 5   | 31   | ns      |
|                                       |                       | 8          | 25,0       | 2   | 11   | 14,5         | 2   | 5    | *       |
|                                       |                       | 10         | 70,5       | 2   | 39   | 43,0         | 2   | 23   | ns      |
|                                       | <i>A. longifolia</i>  | 3          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 4          | 1,0        | 5   | 71   | 0,4          | 5   | 138  | ns      |
|                                       |                       | 6          | 13,9       | 5   | 29   | 5,5          | 2   | 138  | ns      |
|                                       |                       | 8          | 36,0       | 2   | 28   | 25,0         | 2   | 62   | ns      |
|                                       |                       | 10         | 65,0       | 2   | 33   | 49,0         | 2   | 32   | ns      |
|                                       |                       | 15         | 84,6       | 5   | 20   | 71,8         | 5   | 71   | ns      |
|                                       | <i>A. melanoxylon</i> | 3          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 4          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 6          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 8          | 25,5       | 2   | 31   | 0,0          | 2   | 0    | *       |
|                                       |                       | 10         | 18,0       | 2   | 63   | 0,5          | 2   | 142  | ns      |
|                                       |                       | 15         | 32,4       | 5   | 51   | 26,8         | 5   | 51   | ns      |
|                                       | <i>A. saligna</i>     | 3          | 0,0        | 5   | 0    | 0,0          | 5   | 0    | ns      |
|                                       |                       | 4          | 2,2        | 5   | 50   | 1,0          | 5   | 71   | ns      |
|                                       |                       | 6          | 7,2        | 5   | 37   | 6,0          | 5   | 26   | ns      |
|                                       |                       | 8          | 13,5       | 2   | 26   | 18,5         | 2   | 27   | ns      |
|                                       |                       | 10         | 31,0       | 2   | 68   | 26,0         | 2   | 44   | ns      |
| Total<br>leaf +<br>phyllode<br>number | <i>A. cyclops</i>     | 3          | 2,8        | 5   | 30   | 2,2          | 5   | 21   | ns      |
|                                       |                       | 4          | 4,4        | 5   | 13   | 3,0          | 5   | 24   | ***     |
|                                       |                       | 6          | 9,0        | 5   | 22   | 8,6          | 5   | 21   | ns      |
|                                       |                       | 8          | 25,5       | 2   | 8    | 18,0         | 2   | 16   | ns      |
|                                       |                       | 10         | 71,0       | 2   | 38   | 45,0         | 2   | 22   | ns      |
|                                       |                       |            |            |     |      |              |     |      |         |
|                                       | <i>A. longifolia</i>  | 3          | 3,8        | 5   | 12   | 2,6          | 5   | 21   | ***     |
|                                       |                       | 4          | 5,0        | 5   | 14   | 3,8          | 5   | 34   | ns      |



| Parameter | Species                                                             | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signif. |
|-----------|---------------------------------------------------------------------|------------|------------|-----|------|--------------|-----|------|---------|
|           |                                                                     |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |         |
|           | <i>A. melanoxylon</i>                                               | 6          | 17,6       | 5   | 22   | 9,5          | 2   | 37   | *       |
|           |                                                                     | 8          | 37,0       | 2   | 31   | 29,5         | 2   | 60   | ns      |
|           |                                                                     | 10         | 65,0       | 2   | 33   | 53,0         | 2   | 29   | ns      |
|           |                                                                     | 15         | 84,6       | 5   | 20   | 71,8         | 5   | 71   | ns      |
|           |                                                                     | 3          | 4,2        | 5   | 20   | 3,8          | 5   | 22   | ns      |
|           |                                                                     | 4          | 6,6        | 5   | 8    | 5,4          | 5   | 28   | ns      |
|           |                                                                     | 6          | 20,0       | 5   | 18   | 12,0         | 5   | 17   | ****    |
|           |                                                                     | 8          | 53,0       | 2   | 13   | 20,5         | 2   | 4    | **      |
|           |                                                                     | 10         | 53,5       | 2   | 20   | 33,0         | 2   | 39   | ns      |
|           |                                                                     | 15         | 41,6       | 5   | 31   | 46,6         | 5   | 44   | ns      |
|           | <i>A. saligna</i>                                                   | 3          | 5,0        | 5   | 14   | 5,2          | 5   | 9    | ns      |
|           |                                                                     | 4          | 8,6        | 5   | 21   | 7,0          | 5   | 17   | ns      |
|           |                                                                     | 6          | 8,6        | 5   | 46   | 11,0         | 5   | 20   | ns      |
|           |                                                                     | 8          | 13,5       | 2   | 26   | 18,5         | 2   | 27   | ns      |
|           |                                                                     | 10         | 31,0       | 2   | 68   | 26,0         | 2   | 44   | ns      |
|           | Total <sup>3</sup><br>foliage<br>surface<br>area (cm <sup>2</sup> ) | 3          | 11         | 5   | 27   | 6            | 5   | 11   | ns      |
|           |                                                                     | 4          | 18         | 5   | 10   | 11           | 5   | 5    | **      |
|           |                                                                     | 6          | 185        | 5   | 9    | 87           | 5   | 8    | **      |
|           |                                                                     | 8          | 444        | 2   | 14   | 361          | 2   | 9    | ns      |
|           |                                                                     | 10         | 2 559      | 2   | 33   | 1 846        | 2   | 40   | ns      |
|           | Total<br>foliage<br>surface<br>area (cm <sup>2</sup> )              | 3          | 7          | 5   | 20   | 4            | 5   | 31   | ns      |
|           |                                                                     | 4          | 11         | 5   | 13   | 8            | 5   | 7    | ns      |
|           |                                                                     | 6          | 101        | 5   | 22   | 68           | 2   | 53   | ns      |
|           |                                                                     | 8          | 384        | 2   | 6    | 408          | 2   | 25   | ns      |
|           |                                                                     | 10         | 1 190      | 2   | 5    | 1 242        | 2   | 34   | ns      |
|           |                                                                     | 15         | 1 248      | 5   | 15   | 2 015        | 5   | 39   | ns      |
|           | <i>A. melanoxylon</i>                                               | 3          | 3          | 5   | 16   | 5            | 5   | 17   | ns      |
|           |                                                                     | 4          | 14         | 5   | 16   | 16           | 5   | 8    | ns      |
|           |                                                                     | 6          | 115        | 5   | 12   | 152          | 5   | 18   | ns      |
|           |                                                                     | 8          | 386        | 2   | 19   | 410          | 2   | 18   | ns      |
|           |                                                                     | 10         | 769        | 2   | 22   | 1 085        | 2   | 34   | ns      |
|           |                                                                     | 15         | 554        | 5   | 15   | 1 812        | 5   | 31   | ns      |
|           | <i>A. saligna</i>                                                   | 3          | 6          | 5   | 13   | 8            | 5   | 3    | *       |
|           |                                                                     | 4          | 28         | 5   | 20   | 18           | 5   | 15   | ns      |
|           |                                                                     | 6          | 243        | 5   | 28   | 137          | 5   | 24   | ns      |
|           |                                                                     | 8          | 536        | 2   | 25   | 410          | 2   | 18   | ns      |
|           |                                                                     | 10         | 1 455      | 2   | 62   | 2 053        | 2   | 39   | ns      |

<sup>3</sup> Includes both dorsal & ventral surfaces

| Parameter                                       | Species                  | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signif. |
|-------------------------------------------------|--------------------------|------------|------------|-----|------|--------------|-----|------|---------|
|                                                 |                          |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |         |
| Foliage inclination (degrees from the vertical) | <i>A. cyclops</i>        | 10         | 18,0       | 2   | 8    | 29,0         | 2   | 5    | **      |
|                                                 |                          | 15         | 21,6       | 5   | 33   | 29,0         | 5   | 36   | ns      |
|                                                 | <i>A. longifolia</i>     | 10         | 27,8       | 2   | 22   | 50,8         | 2   | 19   | ns      |
|                                                 |                          | 15         | 14,8       | 5   | 20   | 40,6         | 5   | 24   | ***     |
|                                                 | <i>A. melanoxylon</i>    | 10         | 20,3       | 2   | 19   | 58,0         | 2   | 24   | ns      |
|                                                 |                          | 15         | 16,9       | 5   | 20   | 41,7         | 5   | 25   | ****    |
|                                                 | <i>A. saligna</i>        | 10         | 31,5       | 2   | 11   | 49,0         | 2   | 9    | *       |
|                                                 |                          | 15         | 34,7       | 3   | 37   | 50,7         | 3   | 8    | ns      |
|                                                 | <i>A. cyclops</i>        | 10         | 18         | 2   | 0    | 21           | 2   | 2    | ns      |
|                                                 |                          | 15         | 13         | 5   | 14   | 16           | 5   | 11   | ns      |
| Inter-node length (mm)                          | <i>A. longifolia</i>     | 10         | 11         | 2   | 13   | 17           | 2   | 3    | *       |
|                                                 |                          | 15         | 13         | 5   | 14   | 16           | 5   | 11   | ns      |
|                                                 | <i>A. melanoxylon</i>    | 10         | 18         | 2   | 0    | 22           | 2   | 5    | ns      |
|                                                 |                          | 15         | 17         | 5   | 13   | 22           | 5   | 10   | ns      |
|                                                 | <i>A. saligna</i>        | 10         | 19         | 2   | 14   | 36           | 2   | 8    | *       |
|                                                 |                          | 15         | 17         | 5   | 13   | 22           | 5   | 10   | ns      |
|                                                 | <i>A. cyclops</i>        | 10         | 6,5        | 2   | 8    | 6,0          | 2   | 0    | ns      |
|                                                 |                          | 15         | 6,2        | 5   | 19   | 4,4          | 5   | 42   | ns      |
|                                                 | <i>A. longifolia</i>     | 10         | 6,5        | 2   | 8    | 6,5          | 2   | 8    | ns      |
|                                                 |                          | 15         | 6,2        | 5   | 19   | 4,4          | 5   | 42   | ns      |
| Lateral shoot number                            | <i>A. melanoxylon</i>    | 10         | 17,0       | 2   | 6    | 3,0          | 2   | 0    | ***     |
|                                                 |                          | 15         | 7,8        | 5   | 12   | 7,2          | 5   | 23   | ns      |
|                                                 | <i>A. saligna</i>        | 10         | 5,5        | 2   | 27   | 3,5          | 2   | 43   | ns      |
|                                                 |                          | 15         | 28         | 5   | 7    | 21           | 5   | 9    | *       |
|                                                 | <i>A. longifolia</i>     | 15         | 28         | 5   | 5    | 23           | 5   | 9    | ns      |
|                                                 |                          | 15         | 28         | 5   | 5    | 23           | 5   | 9    | ns      |
|                                                 | <i>A. melanoxylon</i>    | 10         | 17,0       | 2   | 6    | 3,0          | 2   | 0    | ***     |
|                                                 |                          | 15         | 7,8        | 5   | 12   | 7,2          | 5   | 23   | ns      |
|                                                 | <i>A. saligna</i>        | 10         | 5,5        | 2   | 27   | 3,5          | 2   | 43   | ns      |
|                                                 |                          | 15         | 28         | 5   | 7    | 21           | 5   | 9    | *       |
| Basal stem circumference (mm)                   | Mean of 4 Acacia species | 15         | 28         | 5   | 5    | 23           | 5   | 9    | ns      |
|                                                 |                          | 15         | 28         | 5   | 5    | 23           | 5   | 9    | ns      |
| Moisture content (%)                            | Mean of 4 Acacia species | 10         | 66,4       | 8   | 1    | 73,9         | 8   | 2    | *       |
|                                                 |                          | 10         | 55,0       | 8   | 4    | 57,4         | 8   | 4    | ns      |
|                                                 |                          | 10         | 78,8       | 8   | 3    | 73,9         | 8   | 5    | ns      |
| Foliage                                         |                          | 10         | 66,4       | 8   | 1    | 73,9         | 8   | 2    | *       |
| Stem                                            |                          | 10         | 55,0       | 8   | 4    | 57,4         | 8   | 4    | ns      |
| Root                                            |                          | 10         | 78,8       | 8   | 3    | 73,9         | 8   | 5    | ns      |

| Parameter                                  | Species                     | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signif. |
|--------------------------------------------|-----------------------------|------------|------------|-----|------|--------------|-----|------|---------|
|                                            |                             |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |         |
| Root<br>surface<br>area (cm <sup>2</sup> ) | <i>A. cyclops</i>           | 3          | 25         | 5   | 30   | 12           | 5   | 23   | ****    |
|                                            |                             | 4          | 63         | 5   | 29   | 31           | 5   | 31   | ***     |
|                                            |                             | 6          | 224        | 5   | 8    | 99           | 5   | 27   | ****    |
|                                            | <i>A. longi-<br/>folia</i>  | 3          | 16         | 5   | 39   | 11           | 5   | 35   | ns      |
|                                            |                             | 4          | 47         | 5   | 24   | 24           | 5   | 18   | ****    |
|                                            |                             | 6          | 145        | 5   | 46   | 62           | 5   | 62   | ns      |
|                                            | <i>A. melan-<br/>oxylon</i> | 3          | 12         | 5   | 21   | 7            | 5   | 46   | **      |
|                                            |                             | 4          | 32         | 5   | 33   | 20           | 5   | 18   | *       |
|                                            |                             | 6          | 107        | 5   | 29   | 76           | 5   | 33   | ns      |
|                                            | <i>A. saligna</i>           | 3          | 30         | 5   | 18   | 17           | 5   | 23   | ns      |
|                                            |                             | 4          | 97         | 5   | 13   | 30           | 5   | 62   | ****    |
|                                            |                             | 6          | 172        | 5   | 19   | 140          | 5   | 37   | ns      |
| Root<br>dry<br>mass (g)                    | <i>A. cyclops</i>           | 3          | 0,03       | 5   | 36   | 0,01         | 5   | 17   | ***     |
|                                            |                             | 4          | 0,06       | 5   | 20   | 0,03         | 5   | 36   | ****    |
|                                            |                             | 6          | 0,48       | 5   | 9    | 0,13         | 5   | 32   | ****    |
|                                            |                             | 8          | 2,28       | 2   | 11   | 0,51         | 2   | 58   | **      |
|                                            |                             | 10         | 4,91       | 2   | 26   | 1,50         | 2   | 66   | ns      |
|                                            | <i>A. longi-<br/>folia</i>  | 3          | 0,04       | 5   | 47   | 0,01         | 5   | 43   | **      |
|                                            |                             | 4          | 0,06       | 5   | 38   | 0,02         | 5   | 35   | **      |
|                                            |                             | 6          | 0,35       | 5   | 11   | 0,11         | 2   | 100  | ****    |
|                                            |                             | 8          | 1,65       | 2   | 3    | 0,83         | 2   | 36   | ***     |
|                                            |                             | 10         | 2,37       | 2   | 8    | 1,11         | 2   | 14   | **      |
|                                            | <i>A. melan-<br/>oxylon</i> | 3          | 0,02       | 5   | 33   | 0,01         | 5   | 42   | *       |
|                                            |                             | 4          | 0,05       | 5   | 28   | 0,04         | 5   | 33   | ns      |
|                                            |                             | 6          | 0,26       | 5   | 35   | 0,14         | 5   | 71   | ns      |
|                                            |                             | 8          | 2,40       | 2   | 34   | 1,38         | 2   | 10   | ns      |
|                                            |                             | 10         | 4,47       | 2   | 8    | 1,13         | 2   | 27   | **      |
|                                            | <i>A. saligna</i>           | 3          | 0,02       | 5   | 20   | 0,02         | 5   | 12   | ns      |
|                                            |                             | 4          | 0,10       | 5   | 29   | 0,03         | 5   | 64   | ****    |
|                                            |                             | 6          | 0,57       | 5   | 58   | 0,18         | 5   | 44   | ****    |
|                                            |                             | 8          | 2,70       | 2   | 37   | 2,36         | 2   | 8    | ns      |
|                                            |                             | 10         | 8,40       | 2   | 74   | 3,24         | 2   | 28   | ns      |
| Nodule<br>number                           | <i>A. cyclops</i>           | 3          | 2,4        | 5   | 112  | 0,2          | 5   | 225  | ns      |
|                                            |                             | 4          | 2,0        | 5   | 50   | 1,4          | 5   | 81   | ns      |
|                                            |                             | 6          | 3,8        | 5   | 43   | 3,4          | 5   | 94   | ns      |
|                                            |                             | 8          | 5,5        | 2   | 90   | 4,5          | 2   | 110  | ns      |
|                                            | <i>A. longi-<br/>folia</i>  | 3          | 7,4        | 5   | 55   | 3,8          | 5   | 82   | ns      |
|                                            |                             | 4          | 8,6        | 5   | 24   | 4,6          | 5   | 45   | **      |

| Parameter                      | Species               | Age<br>mth | Sun-plants |     |      | Shade-plants |     |      | Signif. |
|--------------------------------|-----------------------|------------|------------|-----|------|--------------|-----|------|---------|
|                                |                       |            | Mean       | (n) | C.V. | Mean         | (n) | C.V. |         |
| Nodule<br>dry<br>mass (g)      | <i>A. melanoxylon</i> | 6          | 12.6       | 5   | 78   | 14.5         | 2   | 5    | ns      |
|                                |                       | 8          | 32.5       | 2   | 67   | 45.5         | 2   | 36   | ns      |
|                                |                       | 3          | 3.0        | 5   | 125  | 1.2          | 5   | 108  | ns      |
|                                |                       | 4          | 7.4        | 5   | 31   | 4.0          | 5   | 61   | ns      |
|                                |                       | 6          | 12.2       | 5   | 41   | 21.8         | 5   | 66   | ns      |
|                                |                       | 8          | 32.5       | 2   | 15   | 27.5         | 2   | 23   | ns      |
|                                | <i>A. saligna</i>     | 3          | 1.8        | 5   | 114  | 1.8          | 5   | 121  | ns      |
|                                |                       | 4          | 2.0        | 5   | 0    | 1.8          | 5   | 47   | ns      |
|                                |                       | 6          | 6.6        | 5   | 50   | 4.6          | 5   | 73   | ns      |
|                                |                       | 8          | 25.5       | 2   | 97   | 08.5         | 2   | 64   | ns      |
|                                | <i>A. cyclops</i>     | 8          | 0.27       | 2   | 62   | 0.06         | 2   | 83   | ns      |
|                                |                       | 10         | 0.56       | 2   | 11   | 0.25         | 2   | 60   | ns      |
|                                | <i>A. longifolia</i>  | 8          | 0.18       | 2   | 3    | 0.08         | 2   | 25   | ns      |
|                                |                       | 10         | 0.27       | 2   | 13   | 0.16         | 2   | 28   | ns      |
| Nodule<br>dry<br>mass (g)      | <i>A. melanoxylon</i> | 8          | 0.29       | 2   | 24   | 0.06         | 2   | 50   | ns      |
|                                |                       | 10         | 0.32       | 2   | 2    | 0.13         | 2   | 15   | **      |
|                                | <i>A. saligna</i>     | 8          | 0.22       | 2   | 14   | 0.13         | 2   | 23   | ns      |
|                                |                       | 10         | 0.35       | 2   | 44   | 0.24         | 2   | 54   | ns      |
| Whole<br>plant dry<br>mass (g) | <i>A. cyclops</i>     | 3          | 0.08       | 5   | 35   | 0.04         | 5   | 5    | ***     |
|                                |                       | 4          | 0.18       | 5   | 27   | 0.08         | 5   | 23   | ***     |
|                                |                       | 6          | 1.53       | 5   | 17   | 0.47         | 5   | 6    | ****    |
|                                |                       | 8          | 7.66       | 2   | 18   | 2.63         | 2   | 15   | *       |
|                                |                       | 10         | 16.31      | 2   | 34   | 7.45         | 2   | 75   | ns      |
|                                | <i>A. longifolia</i>  | 3          | 0.07       | 5   | 39   | 0.03         | 5   | 37   | ***     |
|                                |                       | 4          | 0.10       | 5   | 34   | 0.05         | 5   | 31   | **      |
|                                |                       | 6          | 0.80       | 5   | 26   | 0.30         | 2   | 80   | *       |
|                                |                       | 8          | 4.80       | 2   | 2    | 3.30         | 2   | 5    | ****    |
|                                |                       | 10         | 6.90       | 2   | 7    | 4.30         | 2   | 1    | ***     |
|                                | <i>A. melanoxylon</i> | 3          | 0.04       | 5   | 29   | 0.31         | 5   | 36   | ns      |
|                                |                       | 4          | 0.09       | 5   | 41   | 0.08         | 5   | 32   | ns      |
|                                |                       | 6          | 0.51       | 5   | 43   | 0.49         | 5   | 55   | ns      |
|                                |                       | 8          | 6.58       | 2   | 21   | 4.98         | 2   | 5    | ns      |
|                                |                       | 10         | 9.12       | 2   | 13   | 3.98         | 2   | 34   | ns      |
|                                | <i>A. saligna</i>     | 3          | 0.04       | 5   | 38   | 0.03         | 5   | 12   | ns      |
|                                |                       | 4          | 0.21       | 5   | 39   | 0.08         | 5   | 41   | ***     |
|                                |                       | 6          | 2.02       | 5   | 37   | 0.67         | 5   | 51   | ***     |
|                                |                       | 8          | 6.95       | 2   | 22   | 7.48         | 2   | 8    | ns      |
|                                |                       | 10         | 19.10      | 2   | 74   | 11.99        | 2   | 33   | ns      |



grasses could be further encouraged by nitrogen fertilization, which does not improve acacia growth (R. Specht, pers. comm.; Schönau, 1971). This method would be more suitable for semi-natural recreation areas than for wilderness.

Partial shading of the semi shade tolerant species, *A. longifolia* and *A. saligna*, should be avoided as this could favour their establishment. The problem of the spread of *A. melanoxylon* into indigenous forest has not been solved, but will probably be reduced by low intensity exploitation of indigenous trees. It is Forestry Department policy to lop selected timber trees in the S. Cape forests before felling them, so as to minimise damage to neighbouring trees (M. Cameron, pers. comm.).

Although the nursery experiment provided information on the relative shade tolerance of the four *Acacia* species tested, clearer results might have been obtained by less frequent measuring of a smaller number of parameters over a larger number of replicates.

The exploitation of shade tolerance has promise as an alternative to chemical control of acacias in the S.W. Cape. Field trials should now be carried out to identify suitable smother crops, and develop ways of using plant and brushwood shade to control acacia regeneration.

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